

NOTES ON GALÁPAGOS EUPHORBIACEAE

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CROTON

As noted by a number of observers (especially Stewart, Proc. Cal. Acad. Sci. IV. 1:206–209, 215–216. 1911), plants of *Croton* are an important component of the woody vegetation of the Galápagos at both low and high elevations; and in the arid zones *Croton* may be the vegetational dominant. Although Andersson (Kongl. Svenska Freg. Eugenies Resa, Bot. 105, 106. 1857) recognized six species of Galápagos *Croton*, Mueller Argoviensis (DC., Prodr. 15(2):604–606. 1866) amalgamated all of the Galápagos taxa into the single species *Croton scouleri*, and later workers such as Robinson and Stewart have followed Mueller's circumscription.

Svenson (Amer. J. Bot. 33:458–460. 1946) not only treated all the Galápagos Crotons as a single species, but combined *C. scouleri* with the South American species *C. rivinifolius* HBK. There is certainly a striking resemblance between these two species, and Svenson may be correct in postulating that the Galápagos taxa were derived by long-distance dispersal from Ecuadorian populations of *C. rivinifolius*. However, the Galápagos plants differ from the mainland ones in a number of respects, especially in the seeds, which are smooth to pitted rather than ribbed as in *C. rivinifolius* and related species. Consequently, it seems best to follow Mueller and retain *C. scouleri* as a distinct polytypic species endemic to the Galápagos. The system of subspecific taxa presented here to some extent resembles that of J. T. Howell, who examined and annotated a large number of collections, but did not publish his conclusions.

The variation in Galápagos *Croton* is still not satisfactorily understood despite the rather considerable number of collections made of these common plants. Unfortunately, many collectors have not carefully noted the habitat conditions or even the altitude at which specimens were taken, so that it is difficult to establish the ecological status of the various proposed taxa. Most of the characters of the taxa recognized here appear to represent segments of altitudinal clines, and only future work can establish whether or not sufficient discontinuities exist to justify maintaining discrete taxa. Inter-island variation is on the whole less well-defined than altitudinal intra-island variation, but one population at least appears to have a distinct seed size. Nevertheless, even seed size is not consistently diagnostic. It is possible that when the local populations are more thoroughly collected any attempt to recognize varieties within the species will have to be abandoned.

The Galápagos populations of *Croton* may be summarized as follows.

CROTON SCOULERI Hook. f., Trans. Linn. Soc. London 20:188. 1947. Lectotype, Isla San Salvador (James), *Scouler* (K-n. v., A-isotype fragment).

The populations of this species endemic to the Galápagos are here classified into four rather ill-defined varieties.

CROTON SCOULERI var. SCOULERI. *C. macraei* Hook. f., Trans. Linn. Soc. London 20: 188. 1847. Type, Isla Isabela (Albemarle), *Macrae* (K-n. v.). *C. albescens* Anderss., Kongl. Vetensk. Acad. Handl. 1853: 242. 1855. Type, Isla Santa María (Charles), in 'locis editioribus umbrosis', *Andersson 208* (A-fragment of type from S.). *C. incanus* Anders., Kongl. Vetensk. Acad. Handl. 1853:243. 1855 (non *C. incanus* HBK.). Type, Isla San Salvador (James), in 'locis siccis', *Andersson* (GH-isotype). *C. scouleri* var. *glabriusculus* Stewart, Proc. Calif. Acad. Sci. IV. 1:89. 1911. Type, Isla Pinta (Abingdon), 1000–1650 ft., *Stewart 1834* (CAS). *C. scouleri* var. *castellanus* Svenson, Amer. J. Bot. 22:239. 1935. Type, Isla Genovesa (Tower), *Snodgrass & Heller* (GH-n. v.; no collection of Snodgrass and Heller from Genovesa was seen among the Gray Herbarium specimens, and Svenson may have based the name on the Genovesa collection of Baur).

Illustrations. Svenson, Amer. J. Bot. 22: pl. 4, figs. 1–3; pl. 9, figs 1, 2. 1935.

The majority of lowland *Croton* populations belong to this highly diverse variety. The variation in leaf shape from narrowly linear to elliptic is so striking that all previous authors have accepted the narrow-leaved variant as either a species, *C. macraei*, or a variety. However, this foliar variation appears to be at least partly related to an altitudinal cline, linear-leaved plants in the lowlands being replaced by broad-leaved ones at higher elevations. At some localities (Academy Bay, Isla Santa Cruz) narrow- and broad-leaved forms evidently occur in the same population. The transition between the extremes is so continuous that it seems quite impractical to recognize the narrow-leaved plants as a distinct variety. These stenophyllous variants must be classified only at the rank of forma.

CROTON SCOULERI f. *macraei* (Hook. f.) Webster, comb. nov., based on *C. macraei* Hook. f., cited above.

It is possible that the littoral populations with broad densely stellate leaves, designated as var. *castellanus* by Svenson, may prove to merit varietal recognition, particularly if they prove to be characterized by large seed size (see discussion under var. *darwinii*). However, on the basis of presently available specimens no useful diagnostic characters can be found. The only other outstanding variant of var. *scouleri* is the plant from Isla Pinta described as var. *glabriusculus* by Stewart. The type specimen (*Stewart 1834*) is indeed unique in having stellate hairs with one very long branch on the upper leaf surfaces. However, other specimens from Isla Pinta do not show this character, so the taxon described by Stewart does not appear to make up a discrete population. It may be conveniently referred to at the rank of forma.

CROTON SCOULERI f. **glabriusculus** (Stewart) Webster, comb. nov., based on *C. scouleri* var. *glabriusculus* Stewart, cited above.

CROTON SCOULERI var. **darwinii** Webster, var. nov. Frutex vel arbuscula foliis rotundatis depresso-stellatis, seminibus 3.9–4.5 mm longis.

Type. Isla Darwin (Culpepper), *J. R. Hendrickson* H-7, Jan. 29, 1964 (DS-holotype).

This variety is apparently restricted to the two small northernmost islands, Darwin and Wolf. Some forms of var. *scouleri* are similar in leaf shape and pubescence, but these have smaller seeds (2.6–3.6 mm long). One problematical collection from Isla Daphne (*Pool 290*, BKL) has large seeds over 5 mm long but is vegetatively similar to plants described from Genovesa and elsewhere by Svenson as var. *castellanus*. Although Svenson's variety has here been synonymized with var. *scouleri*, it might prove to be characterized by large seed size, and it is possible that var. *darwinii* would then fall into synonymy under var. *castellanus*. However, until more complete collections are available, this possibility must remain only hypothetical. The plants from Isla Darwin and Isla Wolf in any event have a characteristic aspect, and in the present rudimentary state of our knowledge it seems most reasonable to treat them as a distinct variety.

CROTON SCOULERI var. **BREVI-FOLIUS** (Anderss.) Muell.-Arg., in DC., Prodr. 15(2): 605. 1866. *C. brevifolius* Anderss., Kongl. Vetensk. Acad. Handl. 1853:105. 1855. Type, Isla Santa María (Charles), *Andersson 206* (A-fragment of type from S).

As here circumscribed, this variety is restricted to higher altitudes on Isla Santa María. Although Stewart (Proc. Calif. Acad. Sci. IV. 1:88–89. 1911) recorded this variety from a large number of islands, most of the collections cited are here referred to var. *scouleri*. As presently understood, var. *brevifolius* may be distinguished from var. *scouleri* by the loose tomentum on the undersides of the leaves, and from vars. *darwinii* and *grandifolius* by its smaller seeds.

CROTON SCOULERI var. **GRANDIFOLIUS** Muell. Arg., in DC., Prodr. 15(2):605. 1866. Type, Isla San Salvador (James), *Darwin* (CGE-isotype, K-holotype–n. v.).

Illustration. Svenson, Amer. J. Bot. 22:272, pl. 4, fig. 5. 1935.

Most plants of Galápagos *Croton* with large leaves (at least 5 cm long and 3 cm broad) may be assigned to this variety, which is recorded from higher altitudes on Isla Isabela, Isla San Cristóbal, Isla Santa Cruz, and Isla San Salvador. In general, specimens of var. *grandifolius* are easily distinguished from those of vars. *darwinii* and *scouleri* by the larger leaves with flocculent tomentum beneath. It is much more difficult to find good diagnostic characters to separate var. *grandifolius* from var. *brevifolius*, although the leaves are usually smaller in the latter. Some specimens from Isla Santa María (*Howell 9312*, *Stewart 1837*) overlap

var. *grandifolius* in size. The seeds of var. *grandifolius* on Isla Santa Cruz appear to be larger, but the seeds of the large-leaved populations on Isabela, San Cristóbal, and San Salvador are still unknown. Until fruiting collections are available, varietal assignment of the specimens from those three islands must remain provisional.

ACALYPHA

In his synopsis of Galápagos *Acalypha*, Robinson (Proc. Amer. Acad. Arts 38: 161–165. 1902) recognized no less than 13 species, including four described by himself. Pax and Hoffmann (Pflanzenreich IV. 147 (XVI): 30–31, 132–134. 1924) accepted all 13 of Robinson's species and placed them into two widely separated taxa: 'sect.' *Phleoideae* in 'ser.' *Polygynae-Acrogynae*, and 'sect.' *Cuspidatae* in 'ser.' *Oligogynae*. This disposition, apparently made on the basis of position of spikes, terminal or axillary, resulted in a completely artificial arrangement of taxa and is wholly untenable, however the species may be circumscribed.

The treatments of Robinson and of Pax and Hoffmann contrast strongly with the earlier one of Mueller Argoviensis, who treated all of the Galápagos taxa of *Acalypha* known to him as seven varieties of the single species *A. parvula*. A detailed analysis of the much larger number of specimens now available shows that Mueller was justified in lumping together under *A. parvula* many of the populations of plants with glandular trichomes. However, the populations of plants with more densely pubescent leaves and stems lacking glandular trichomes do not appear to intergrade with members of the *A. parvula* complex on the several islands where they are sympatric. These non-glandular plants are therefore accepted as distinct species. The newly described *A. wigginsii* is to some extent intermediate between *A. parvula* and *A. sericea* and is sympatric with them on Isla Santa Cruz. The classification thus adopted here, with five species and several varieties, represents a rather unstable compromise between the previous schemes. It, like its predecessors, may have to be extensively remodeled when better population samples are available of these still rather poorly understood taxa.

*Glandular trichomes absent or nearly so;
young stems densely villose-hirsute*

ACALYPHA SERICEA Anderss., Kongl. Vetensk. Acad. Handl. 1853:238. 1855.

This is the most widespread and variable non-glandular species, corresponding to *A. parvula* in the glandular taxa. The species comprises 3 fairly well-marked varieties differing in mean size of leaves, staminate spikes, and seeds.

ACALYPHA SERICEA Anderss. var. SERICEA. *A. parvula* γ *pubescens* Muell.-Arg., Linnaea 34:47. 1865; in. DC., Prodr. 15(2):878. 1866. Type, Isla Isabela, 'locis lapidosis regionis inferioris insulae Albemarle', Andersson (S-n. v.). The type locality was originally cited as Isla San

Cristóbal (Chatham), but was corrected in Andersson's later treatment (Kongl. Svenska Freg. Eugenies Resa, Bot. 103. 1857).

Leaves 1–2 (–3) cm long, with mostly 10–15 teeth per side; staminate spikes mostly 3–15 mm long; seeds 1.0–1.2 mm long. Recorded from Marchena (Bindloe) and Pinta (Abingdon); some specimens from Abingdon are unusually glandular and somewhat approach *A. parvula*.

ACALYPHA SERICEA Anderss. var. *indefessus* Webster, var. nov. Suffrutex caulibus villosulis eglandulosis, foliis 2.5–5.5 longis, dentibus lateribus c. 15–25, spicis masculis plerumque 5–15 mm longis, seminibus 1.2–1.3 mm longis.

Type. Isla Santa Cruz (Indefatigable), along 'new road' from Bahia Academy to Bella Vista, transition zone, *Wiggins 18672*, Feb. 9, 1964, (DS-holotype). Other collections examined, all from the general locality, include *Fournier 243* (DAV), *Taylor TT59* (CAS), and *Wiggins 18492* (DS).

Endemic to Isla Santa Cruz, in relatively mesic vegetation between 100 and 200 m. The plants resemble var. *baurii* from San Cristóbal in aspect, but have much shorter staminate spikes and styles; the larger seeds and leaves (with more teeth per side) provide differential features from var. *sericea*.

ACALYPHA SERICEA Anderss. var. *baurii* (Robins. & Greenm.) Webster, comb. nov. *A. baurii* Robins. & Greenm., Amer. J. Sci. 50:144. 1895. Type, Isla San Cristóbal (Chatam), southwest end, middle region, *Baur 285* (GH).

Leaves mostly 4–6 cm long, with 23–31 teeth per side; staminate spikes 30–60 mm long; seeds 1.2 mm long. Known only from the type collection on San Cristóbal.

ACALYPHA FLACCIDA Hook. f., Trans. Linn. Soc. London 20:186. 1847. *A. parvula* η *flaccida* Muell.-Arg., Linnaea 34:48. 1865; in DC., Prodr. 15(2): 878. 1866. Type, Isla San Salvador (James), *Darwin* (CGE).

Known only from the type collection; very similar to *A. sericea* in appearance, but with much smaller, non-hispidulous pistillate bracts in strictly axillary spikes.

ACALYPHA VELUTINA Hook. f., Trans. Linn. Soc. London 20:186. 1847. *A. parvula* γ *pubescens* ξ *velutina* Muell.-Arg., Linnaea 34:48. 1865; in DC., Prodr. 15(2):878. 1866. Type, Isla Santa María (Charles), *Darwin* (CGE). The variety recognized by Hooker, *A. velutina* β *minor* (Trans. Linn. Soc. London 20:187. 1847), also based on a Darwin collection from Charles (CGE), is only a small-leaved form of no taxonomic importance.

Very similar to some forms of *A. sericea*, but differing in the axillary spikes and distinctly bullate-rugose leaves. Endemic to Isla Santa María.

Glandular trichomes present, at least on pistillate bracts

Acalypha wigginsii Webster, sp. nov. Annu erecta, caule dense glanduloso-tomentello; foliis ovatis basi cordatis obtuse dentatis 2–7 cm longis,

strigoso-hirsutis glandulosisve; spicis axillaribus, parte mascula 1.5–10 mm longa; calycis masculis glabris; involucris foemineis 2–3, 2-floris, ad mediam 6–10-lobis, glandulosis, parce hirsutis; seminibus 1.3–1.5 mm longis.

Type. Isla Santa Cruz (Indefatigable), north slope of Mt. Crocker, alt. ca. 860 m, *Wiggins & Porter 663*, Feb. 18, 1967 (DS-holotype). Additional collections examined, Mt. Crocker, *Wiggins & Porter 665* (DS); Gebirge im Innern, *Schimpff 96* (CAS, MO); among rocks in moist zone, south slope of mountain, alt. 1000 ft., *Svenson 96* (BRKL).

This species is known only from Isla Santa Cruz, where it appears to be restricted to higher altitudes in the mountainous interior. The completely glabrous staminate calyces and large stipules distinguish it from the many taxa of the *A. parvula* complex, while the glandular pubescence sets it apart from the large-leaved species related to *A. sericea*.

ACALYPHA PARVULA Hook. f., Trans. Linn. Soc. London, 20:185. 1847.

All of the small-leaved populations of Galápagos *Acalypha* with glandular pubescence are referred to this single protean species. As Robinson noted, these plants include annuals and perennials, erect and prostrate forms, with striking differences in the spikes. His decision to recognize nine species in this complex cannot be followed, because these various marked characters vary in a largely uncorrelated manner from island to island without showing any clear geographic separations. A number of the taxa may be treated as varieties, in approximately the circumscriptions of Mueller, but it must be admitted that these are difficult to distinguish in practice and may not be natural units. The four varieties recognized here are extensively sympatric, and further study may show that they are simply arbitrary assemblages of plants selected from a mosaic of clinal and microgeographic variation.

ACALYPHA PARVULA Hook. f. var. PARVULA. Type, Isla Isabela (Albemarle), *Macrae* (K-n. v.). *A. cordifolia* Hook. f., Trans. Linn. Soc. London 20:187. Type, Isla Santa María (Charles), *Darwin* (CGE). *A. diffusa* Anderss., Kongl. Vetensk. Acad. Handl. 1853:240. 1855. Type, Isla Isabela (Albemarle), 'in locis siccissimis', *Andersson* (GH-isotype). *A. spicata* Anderss., Kongl. Vetensk. Acad. Handl. 1853:239. 1854. Type, Isla San Cristóbal (Chatham), *Andersson* (GH-isotype). *A. parvula* β *cordifolia* Muell.-Arg., *Linnaea* 34:47. 1865; in D.C., *Prodr.* 15(2):877. 1866. *A. albemarlensis* Robins., *Proc. Amer. Acad. Arts* 38:163. 1902. Type, Isla Isabela (Albemarle), Tagus Cove, alt. 1220 m, *Snodgrass & Heller 885* (GH-holotype).

This variety is the most widespread and diverse taxon of Galápagos *Acalypha*. It is recorded from Fernandina, Isabela, Pinzón, San Cristóbal, Santa Cruz, Santa Fé, and Santa María. Only on Española and San Salvador does it appear to be lacking from the larger central islands. Various forms of var. *parvula* are difficult to separate from other varieties of

A. parvula, and sometimes even from specimens of *A. sericea*. However, in the majority of instances the populations included here may be recognized by the axillary pistillate spikes, distinctly glandular erect stems, seeds 1.1 mm long or less, and leaves scarcely exceeding 2 cm long.

ACALYPHA PARVULA var. *RENIFORMIS* (Hook. f.) Muell.-Arg., *Linnaea* 34:48. 1865; in DC., *Prodr.* 15 (2):878. 1866. *A. reniformis* Hook. f., *Trans. Linn. Soc. London* 20:187. 1847. Type, Isla Santa María (Charles), *Darwin* (CGE). *A. adamsii* Robins., *Proc. Amer. Acad. Arts* 38:161. 1902. Type, Isla San Cristóbal (Chatham), southwest end, middle region, *Baur* 282, June 1891 (GH).

Stems often prostrate, usually not densely glandular; terminal spikes usually present; pistillate bracts mostly sessile; seeds small (0.9–1.1 mm long). Recorded from Española, Pinzón, Rábida, San Cristóbal, San Salvador, Santa Cruz, Santa Fé, and Santa María.

ACALYPHA PARVULA Hook. f. var. *STROBILIFERA* (Hook. f.) Muell.-Arg., *Linnaea* 34:47. 1865; in DC., *Prodr.* 15(2):877. 1866. *A. strobilifera* Hook. f., *Trans. Linn. Soc. London* 20:187. 1847. Type, Isla San Cristóbal (Chatham), *Darwin* (CGE). *A. parvula* a *procumbens* Muell.-Arg., *Linnaea* 34:48. 1865; in DC., *Prodr.* 15(2):878. 1866.

Stems usually glandular, spikes terminal or axillary; pistillate bracts usually pedunculate; seeds mostly large (1.2–1.5 mm long). Recorded from Daphne, San Cristóbal and Santa Cruz, common in the vicinity of Academy Bay on the latter island.

ACALYPHA PARVULA Hook. f. var. **chathamensis** (Robins.) Webster, comb. nov. *A. chathamensis* Robins., *Proc. Amer. Acad. Arts* 38:163. 1902. Type, Isla San Cristóbal (Chatham), *Snodgrass & Heller* 541 (GH-lectotype, DS-isotype).

Stems erect, glandular; leaves larger (2.5–4.5 cm long) than in most other forms of *A. parvula*; spikes axillary; seeds small (1.0–1.1 mm long). Endemic to San Cristóbal, where it is known from only one other collection (*Snodgrass & Heller* 540, DS, GH). In aspect, specimens of var. *chathamensis* suggest *A. sericea* var. *baurii*, which also occurs on San Cristóbal; but the glandular and non-velutinous indumentum definitely places them within *A. parvula*.

I wish to thank the curators of the herbaria at Stanford, Harvard, the Brooklyn Botanical Garden, and Cambridge for their generosity in loaning critical specimens. The Darwin collections from the herbarium at Cambridge (CGE) are duplicates of those at Kew examined by Hooker; since the specimens at Kew were not seen, no attempt was made to specify whether the collections at CGE are syntypes or isotypes.

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